Claw Transformation and Regeneration in Adult Snapping Shrimp: Test of the Inhibition Hypothesis for Maintaining Bilateral Asymmetry

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Abstract. In the paired asymmetric claws of adult snapping shrimp, *Alpheus heterochelis*, the minor, or pincer, claw may transform into a major, or snapper, claw if the existing snapper claw is damaged or lost, implying that an intact snapper claw normally inhibits the contralateral pincer claw from advancing to a snapper. We find that the pincer-to-snapper advancement in external form occurs almost immediately after the snapper is lost even as late as the premolt stage. The transforming claw in turn inhibits the newly regenerating pincer claw from becoming a snapper, but if the dactyl of the transforming claw is cut, then snapper-based inhibition is removed and the contralateral claw may regenerate as a snapper, resulting in shrimp with paired snapper claws. However, damaging an established snapper claw will not allow another snapper claw to regenerate at the pincer site, implying that less inhibition is required to restrict a newly regenerating claw to a pincer than to arrest an existing pincer claw. Inhibition may be manifested largely in terms of quantity of innervation. Hence the greater innervation of the snapper side over the pincer side would inhibit the pincer side, accounting for the regeneration of paired claws in their previous configuration following loss of both claws. Loss of the paired claws in two consecutive molts retards their development so that both claws often appear as pincers, but in succeeding molts one usually differentiates into a snapper and bilateral asymmetry is restored. In contrast, shrimp with paired snapper claws retain this configuration over several molts unless one or both of the claws are lost; in that case, regeneration restores bilateral asymmetry. Thus, bilateral asymmetry of the paired claws of adult shrimp is governed by a strong intrinsic lateralizing mechanism in which the snapper claw inhibits the pincer from advancing to another snapper.

Introduction

Among crustaceans, bilateral asymmetry of the first pair of chelipeds is common; one of the paired claws is more enlarged and elaborate (major claw) than the other (minor claw). In snapping shrimps of the family Alpheidae, the major, or snapper, claw is almost as large as the abdomen and has a hammer on the moveable dactyl that fits into a reciprocal socket on the fixed pollex (Fig. 1A) (Przibram, 1901). The closing action of the hammer into the socket is made with such tremendous force that it is accompanied by a loud popping sound and a jet-expulsion of water, both of which are used in agonistic encounters (Hazlett and Winn, 1962; Ritzmann, 1974) or in crushing bivalve shells (McLaughlin, 1982). The minor, or pincer, claw is much smaller and is used in burrowing and feeding.

An unusual feature of claw bilateral asymmetry in snapping shrimp is the ability to reverse its configuration. Loss of the snapper early in an intermolt results in the transformation of the pincer to a snapper and the regeneration of a new pincer at the snapper site at the next molt (Przibram, 1901; Wilson, 1903). In addition to loss of the snapper claw, less drastic measures such as its denervation (Mellon and Stephens, 1978), dactylotomy (Read and Govind, 1997), or closer muscle tenotomy (Govind *et al.*, 1988) are also sufficient to trigger transformation of the pincer into a snapper. Because the existing snapper claws repair themselves, such procedures produce shrimp that possess paired snapper claws. Since these manipulations that induce pincer-to-snapper transformation involve
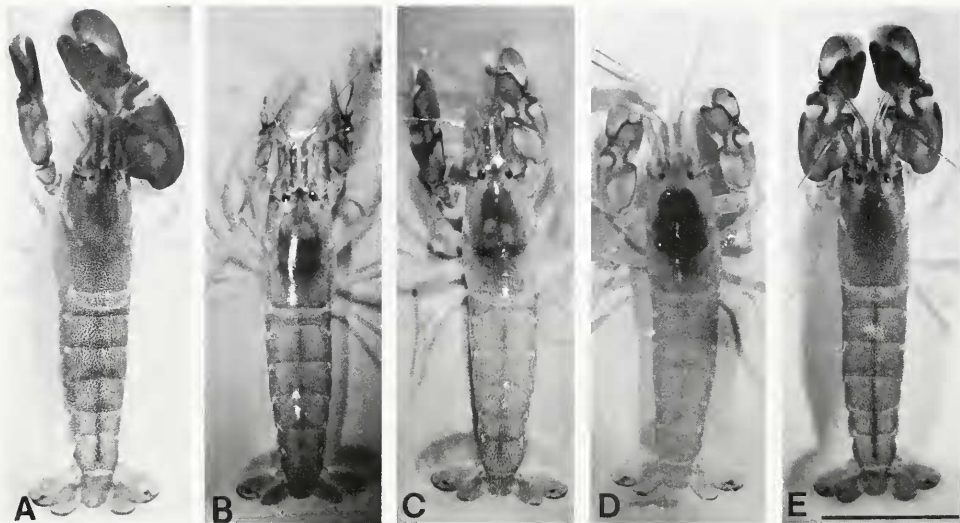
Figure 1. Adult snapping shrimp showing different configurations of their paired claws. (A) Pristine asymmetric configuration in which the snapper (right claw) is extremely hypertrophied, with a pronounced hammer and socket, and the pincer (left claw) is small, slender, and lacks the snapping apparatus. (B) Newly regenerated paired pincer claws which are smaller than their pristine counterparts. (C) Paired snapper claws with newly regenerated snapper (right claw) and dactyl-less transformed pincer (left claw). (D) Newly regenerated paired snapper claws which are much smaller and not as highly differentiated as their pristine counterparts. (E) Pristine paired snapper claws in which the paired claws are similar in size and differentiation. Scale bar 10 mm. ×2.5

damage to the nervous system of the snapper claw, it is likely that the transformation results from loss of the neural inhibition by which the snapper claw prevents the pincer claw from completing its development to a snapper (Wilson, 1903). Because regenerating claws in adult shrimp pass through a distinct pincerlike stage before differentiating into a snapper claw (Wilson, 1903; Darby, 1934; Read and Govind, 1997), we have devised a scheme in which loss of the snapper claw removes its inhibition on the pincer, which then advances to a snapper and in turn inhibits the newly regenerating claw to a pincer.

Snapper-based inhibition of the pincer claw can also explain why loss of the pincer claw in adult shrimp results in the regeneration of another pincer (Wilson, 1903). To explain the fact that simultaneous loss of both claws results in claw regeneration in the same configuration, we would have to assume that snapper-based inhibition prevails even in the absence of claws. Thus, no matter which claw is lost, inhibition by the snapper claw (or its site) on the pincer claw (or its site) ensures regeneration of bilateral asymmetry. A simple and economical scheme for explaining how bilateral asymmetry is maintained in the face of claw loss and regeneration in adult snapping shrimp is that of Wilson (1903), who regarded the pincer

as an arrested snapper. We have adopted this scheme with the assumption that the inhibitory signal has a neural basis. That assumption largely rests on the fact that cutting the nerve in the snapper claw is enough to trigger transformation of the pincer to a snapper. The inhibitory signal may therefore be easily manipulated with minor surgery of the claws. Here we describe experimental manipulations designed to explore some ramifications of the inhibition hypothesis for claw bilateral asymmetry in adult snapping shrimp. Our findings support the existence of a lateralizing mechanism that is based on inhibition from the snapper claw or from its site and can switch from one side to the other.

Materials and Methods

Adult snapping shrimp, *Alpheus heterochelis,* of both sexes were collected at low tides off the coast of Beaufort, North Carolina, and transported to Scarborough, Ontario, where they were held in the laboratory at room temperature, 23°C. The shrimp were housed in 25-liter glass aquaria partitioned into 12 compartments with plastic screening (Young *et al.,* 1994)—one shrimp per compartment. They were fed at 2–3 day intervals with a specially

prepared diet consisting of a mixture of fish, beef heart, carrots, and commercial trout chow. Under these conditions the shrimps had an intermolt period between 19 and 26 days, for an average of 23 days. A detailed molt history was kept for each animal, and in most cases experimental manipulations were carried out 1 or 2 days after ecdysis.

All animals were allowed to molt twice before being selected for study in order to ensure that the claws were fully differentiated (Read and Govind, 1991). Several types of experimental manipulations were made. The simplest one was to induce the animal to autotomize its claw after ecdysis by gently pinching the limb with forceps just distal to the autotomy plane. For more complex manipulations, the shrimp were first anesthetized by cooling; then, either the dactyl of the snapper claw was cut close to its attachment to the claw so that most of it was removed, or the nerve in the snapper claw was sectioned. The latter was accomplished by cutting a small flap of cuticle in the ventral side of the merus and pulling nerve 2 (the larger of two) so that it broke more proximally at the autotomy plane. After a substantial length of nerve 2 had been removed, the cuticular flap was replaced and the shrimp were treated with a wide-spectrum antibiotic (Paragon) for the next two days. Limb immobilization was achieved by anesthetizing the shrimp, then applying cyanoacrylate glue to the thoroughly dried converging edges of the propus and dactyl. Experimental manipulations were usually performed 1–2 days after a molt, and the experimental shrimp were observed over the next two to three intermolts.

Fiber composition of the claw closer muscle was determined by obtaining frozen cross-sections of the claws and staining these histochemically so that standard techniques for detecting myofibrillar ATPase activity (Ogonowski and Lang, 1979) could be applied.

To evaluate the degree of transformation of pincer to snapper claw, a transformation index, based on five morphological features, each representing a graded measure of a unique snapper characteristic, was devised. The first feature, based upon the presence and development of the plunger and socket, was given a weighting of 4 points and determined by comparing the transforming claw with a standard developmental series similar to that in Figure 2. For example, a transforming claw with no plunger or socket (similar to a pristine pincer) would be assigned 0 points, while one with a plunger and socket (similar to a pristine snapper) would be allotted 4 points. The second feature, stoutness, was weighed at 3 points and based upon the ratio of propus length to width. The smaller the ratio, the stouter and more snapper-like the claw, and hence the more points allocated. The last three features were weighted at 1 point each and based upon the presence and development or abundance of the transverse groove, tubercles, and plumose setae (Read and Govind, 1991). The maximum possible transformation index score

was 10, the equivalent of a pristine snapper; the minimum was 0, equivalent to a pristine pincer.
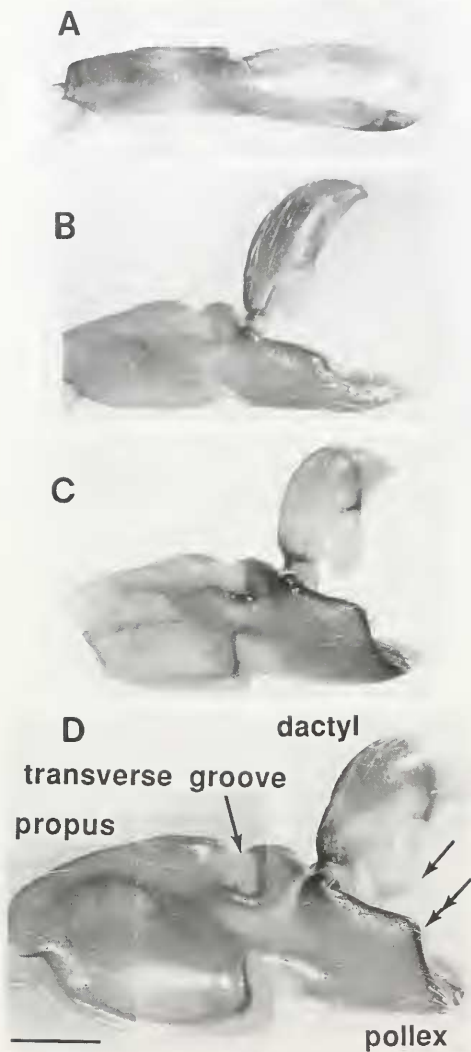
Results

How late in the intermolt can inhibition to the pincer claw be removed?

In most previous studies the snapper was removed a day or two after the shrimp molted, thus providing enough time for transformation and regeneration of claws that, by the next molt, both claws appeared at an advanced state. Can inhibition be removed later in the intermolt, even perhaps as late as the premolt stage? Snappers were autotomized in 37 shrimps at various stages of the molt cycle, as determined by measuring epidermal retraction and setal development in the pleopods (Aiken, 1973); pleopod stages may range from 0 (intermolt) to 5.5 (late premolt). Following ecdysis, the contralateral claws were examined and a transformation index, representing degree of transformation from pincer to snapper (Fig. 2), was calculated on a scale of 0 (the equivalent of a pristine pincer) to 10 (a pristine snapper). The results indicated that the effect of a snapper autotomy on the contralateral pincer was not restricted to the intermolt stage or even the early premolt stage. When done midway or even fairly late into the molt cycle—i.e., as late as pleopod stage 4.0—the pincer in some cases showed clear signs of transformation (Fig. 3). There was a gradation in the effect that was related to the time in premolt when the snapper was autotomized and the interval between the snapper autotomy and the ensuing ecdysis.

In addition, for 9 animals the transforming pincer was selected for histochemical analysis, to characterize the fiber type of the closer muscle. In these shrimp, the snapper had been autotomized at pleopod stages ranging from 0 to 3.5, and the transforming pincers had a transformation index ranging from 2.5 to 6.0. All 9 animals still retained the band of fast muscle that is unique to the pincer (Govind *et al.*, 1986), although in most animals it had begun to degenerate (Fig. 4). Muscle degeneration signifies that transformation had begun even in late premolt shrimp, suggesting that snapper-based inhibition is removed almost immediately and is unrelated to the stage of the molt cycle.
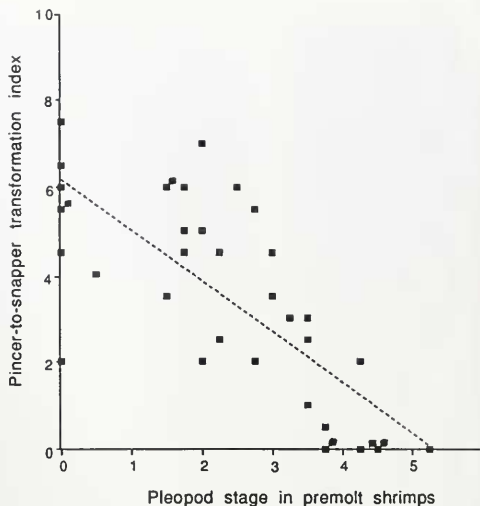
Is an intact transforming claw necessary to limit claw regeneration to a pincer at the contralateral snapper site?

We have shown previously that denervating the transforming pincer claw will allow regeneration of a pincer or a snapper claw at the contralateral snapper site; the appearance of a snapper claw implies the loss of snapper-based inhibition (Young *et al.*, 1994). To pursue this idea further, we wondered whether dactylotomy alone would

Figure 3. Relationship between pleopod stage in premolt shrimp subjected to snapper autotomy and pincer-to-snapper transformation index defined by 0 as pristine pincer and 10 as pristine snapper. The degree to which the pincer transforms is linearly related (regression line) to the stage at which the snapper is removed in premolt shrimps. $N = 37$, $r^2 = 0.577$ ($P < 0.005$), slope $b = -1.162$.

Figure 2. A pristine pincer claw (A) progressively developing *via* two selected stages (B, C) into a pristine snapper claw (D) characterized by a hammer (arrow) and socket (double arrow), a transverse groove, and hypertrophy of the entire claw. The slender pristine pincer claw (A) acquires all the snapper features after the first molt (B), and in subsequent molts (C, D) becomes hypertrophied with further accentuation of the snapper features. Scale bar 3 mm. ×6

be equally effective. Ten animals were successfully manipulated so that the snapper was autotomized and the pincer dactylotomized. In all cases, the pincer transformed into a snapper; *i.e.,* it hypertrophied and developed a socket, despite lacking a dactyl (Table Ia). In 7 of those 10 shrimp, a snapper regenerated on the contralateral side, resulting in a symmetrical animal, albeit one snapper lacked a dactyl (Fig. 1C) and the regenerated snapper often did not grow to pristine proportions. In the other 3 shrimp, a pincer regenerated at the snapper site, resulting in a reversal of asymmetry. Thus pincer dactylotomy, mimicking a mild form of denervation, appeared to be sufficient to remove snapper-based inhibition of the regenerating claw.

Can snapper-based inhibition of a regenerating pincer claw be removed?

Loss of the pincer claw results in the regeneration of another pincer claw presumably because the contralateral snapper restricts regeneration at this site to a pincer (Wilson, 1903). Is it possible to remove this snapper-based inhibition by damaging the snapper when regeneration is taking place at the pincer site? We tested this possibility by removing the pincer claw and at the same time cutting the snapper dactyl. These procedures were successfully accomplished in nine shrimp (Table Ib). At the next molt, a normal-appearing pincer regenerated at the original pincer site in these shrimp. On the contralateral side the
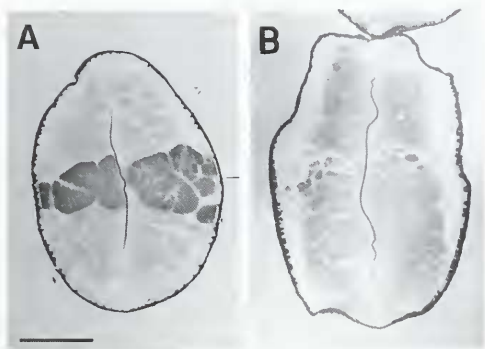
Figure 4. (A) Cross-section of a pristine pincer claw in which the closer muscle, stained histochemically for myofibrillar ATPase, shows a characteristic central band of fast fibers (dark-staining) flanked by slow fibers (light-staining). (B) Cross-section of a pincer claw transforming to a snapper in which fast fibers (dark staining) in the central band have degenerated, while the flanking slow fibers (light staining) are intact. Scale bar 1 mm. ×15

intact snapper showed little regeneration of its cut dactyl for at least two subsequent molts. Snapper dactylotomy did not induce regeneration of a snapper claw at the pincer site.

In an earlier experiment, transecting nerve 2 in the transforming pincer claw permitted regeneration of a snapper claw at the old snapper site, implying the removal of snapper-based inhibition (Young *et al.,* 1994). Therefore, we transected nerve 2 from the autotomy plane to mid-merus in the pristine snapper claw and autotomized the pincer claw at the same time. The procedure was successful in 15 shrimp (Table 1c). None of these animals regenerated a snapper: 7 had regenerated a pincer by the end of the first molt cycle, 12 had a pincer by the end of the second molt cycle, and all had regenerated a pincer by the end of the third molt cycle. In 11 of these animals, snapper function was restored, but to varying degrees: 4 could open and close the dactyl but not snap, 5 could snap weakly, and 3 could snap with moderate force. In most cases, snapper function began returning near the end of the first molt cycle. Thus snapper denervation failed to bring about regeneration of another snapper claw at the pincer site.

Can snapper-side inhibition be weakened to permit regeneration of a snapper at the pincer site?

When both snapper and pincer claws are removed simultaneously, regeneration at these sites is of a similar type claw (Przibram, 1901), suggesting that snapper-based inhibition is present even in the absence of the snapper claw. Can this inhibition present on the snapper

side be weakened to allow regeneration of a second snapper on the contralateral side? We therefore tried removing both snapper and pincer claws at a time when snapper-based inhibition might not be well established. This would be the case immediately after reversal of asymmetry when the newly transformed snapper claw is not as elaborate nor as hypertrophied as a pristine snapper, nor is the newly regenerated pincer claw as well differentiated as the pristine pincer (Przibram, 1901; Wilson, 1903). Forty-seven animals were successfully snapper-autotomized and at the next molt, following a reversal of asymmetry, subjected to a paired autotomy. Relative to the most recent configuration, the location of the pincer and snapper was maintained in 33 and reversed in 14 animals (Table 1d). Despite reversal of bilateral asymmetry, snapper-based inhibition remained intact.

We next tried snapper dactylotomy as a means of inducing pincer transformation. Out of 21 animals, 11 showed transformation of the pincer into a snapper while the damaged snapper repaired itself, resulting in shrimp with paired snapper claws. Following paired autotomy in these 11 animals, 8 regenerated limbs to mimic the original asymmetric configuration, but 3 regenerated double snappers (Table 1e). Both the regenerated snapper claws

Table 1

Configuration of paired claws in snapping shrimp following regeneration at one or both sites in response to various manipulations

| Manipulation | Claw configuration | | | |
	Snapper site	Pincer site	#	%
a. Pincer dactylotomy with snapper autotomy	pincer	snapper	3	30
	snapper	snapper	7	70
b. Pincer autotomy with snapper dactylotomy	snapper	pincer	9	100
c. Pincer autotomy with snapper denervation	snapper	pincer	15	100
d. Snapper autotomy at first molt; paired autotomy at second molt	snapper	pincer	33	70
	pincer	snapper	14	30
e. Snapper dactylotomy at first molt; paired autotomy at second molt	snapper	pincer	8	73
	snapper	snapper	3	27
f. Paired autotomy at first molt; paired autotomy at second molt	snapper	pincer	46	96
	pincer	snapper	1	2
	snapper	snapper	1	2
g. Paired autotomy at first molt; paired autotomy at second molt and snapper-side limb bud immobilized at third molt	snapper	pincer	22	79
	snapper	snapper	6	21

were relatively small in comparison to the animal (Fig. 1D), although the limb on the original snapper side tended to be slightly larger than its counterpart. This was the first demonstration of a snapper claw regenerating at a pincer site with an extant snapper claw on the opposite side.

Can snapper-side inhibition survive successive claw loss?

A newly regenerated limb is usually smaller than a pristine limb, suggesting that the regenerating limb is in an immature state, which could probably be exaggerated with a second round of regeneration. Under these conditions, does snapper-side inhibition still prevail? A group of 48 shrimp were successfully subjected to two consecutive paired autotomies of their claws and the returning asymmetry observed (Fig. 5; Table 1f). After the paired claws had regenerated for the first time, 75% were asymmetric, although they were considerably smaller than the pristine claw; the remainder were no more advanced than stage 5 limb buds or stage 6 pincers (Govind and Read, 1994). After they had regenerated for the second time, they were even smaller. Only 34% showed slight asymmetry, and 66% resembled stage 5 limb buds or stage 6 pincers (Fig. 1B). Over the next two molts, however, these pincer-symmetric shrimp reverted to the original snapper/pincer configuration. Of 48 animals, 46 regenerated limbs to the original configuration, one experienced a reversal, and one regenerated paired snappers. These results show that snapper-based inhibition usually persisted through at least two successive paired autotomies, although occasionally it could be reversed or even absent.

As shown in the above experiment, after two successive paired autotomies the newly regenerated claws were small and the snapper was not highly differentiated. Occasionally only the faintest trace of a snapper—for example, a poorly developed hammer—was seen, and in overall dimension the claw was more like a pincer. To test the possibility that manipulation of the snapper-side limb, even in this relatively immature condition, could reverse claw asymmetry, we performed the following experiment. A group of 28 shrimp were subjected to two consecutive paired autotomies, then the snapper-side limb bud was glued shut, effectively restricting movement of the dactyl of this regenerating limb (Fig. 5; Table 1g). Most (22) of these animals regenerated claws resembling the original configuration. However, six animals regenerated paired snappers, showing that the limb bud at the pincer site was capable of developing into a snapper. When compared to the previous experiment in which regeneration was assessed after two successive paired autotomies, the number of snapper-symmetric shrimps in the present experiment proved to be significant ($X^2 = 5.612$, $P < 0.02$).

Can snapper-symmetry be maintained following claw loss?

The generation of adult shrimp with paired snapper claws by regeneration of a second snapper raises questions about the stability of this unusual condition. These snapper-symmetric shrimp retained their symmetry following a subsequent molt, at which time the second snapper assumed more pristine proportions (Fig. 1E). Symmetry was retained in five shrimp that underwent three subsequent molts, showing that once snapper-symmetry is established, it is retained through later molts. On the other hand, if the second snapper is removed, as was done in three shrimp after they had molted once, the shrimp regenerated a pincer in its place. Even if the second snapper was removed after three molts, as was done in two shrimp, a pincer regenerated in its place. Finally, in five shrimp with similar-sized paired snapper claws, removal of both claws resulted in the regeneration of paired asymmetric claws in the original configuration. Clearly, the snapper-symmetric condition is relatively stable but not permanent, as loss of one or both claws allows regeneration of asymmetric claws.

Discussion

Our experiments produced paired regenerated claws in the usual asymmetric configuration of pincer/snapper as well as, in a few cases, in the unusual symmetric configurations of pincer/pincer or snapper/snapper. The pincer-symmetric condition appears to be ephemeral, because in succeeding molts, given adequate time for development, one of the claws becomes a snapper. In contrast, the snapper-symmetric condition can be maintained over several molts, assuming a relatively permanent state. Indeed, we have maintained snapper-symmetric shrimp for five molts, providing there is no loss of or damage to the claws (Pearce and Govind, 1987). Loss of one or both claws in these snapper-symmetric shrimp immediately restores the asymmetric configuration of the paired claws upon regeneration. The observations that the pincer-symmetric condition is ephemeral and the snapper-symmetric condition is more stable tend to support the view that the pincer represents a stage in the development of the snapper, with the final condition of claw regeneration being that of a snapper (Wilson, 1903; Darby, 1934).

With this developmental sequence in mind, lateralization of the paired claws would be easily achieved if the snapper claw or its putative site arrested the development of the contralateral claw to a pincer state. Although the nature of the inhibitory mechanism is not known, considerable evidence suggests that it has a neural basis and that inhibition is removed most readily with loss of the entire claw but also with nerve transection (Mellon and Stephens, 1978), closer muscle tenotomy (Govind *et al.,* 1988), or dactylotomy (Read and Govind, 1997); in other
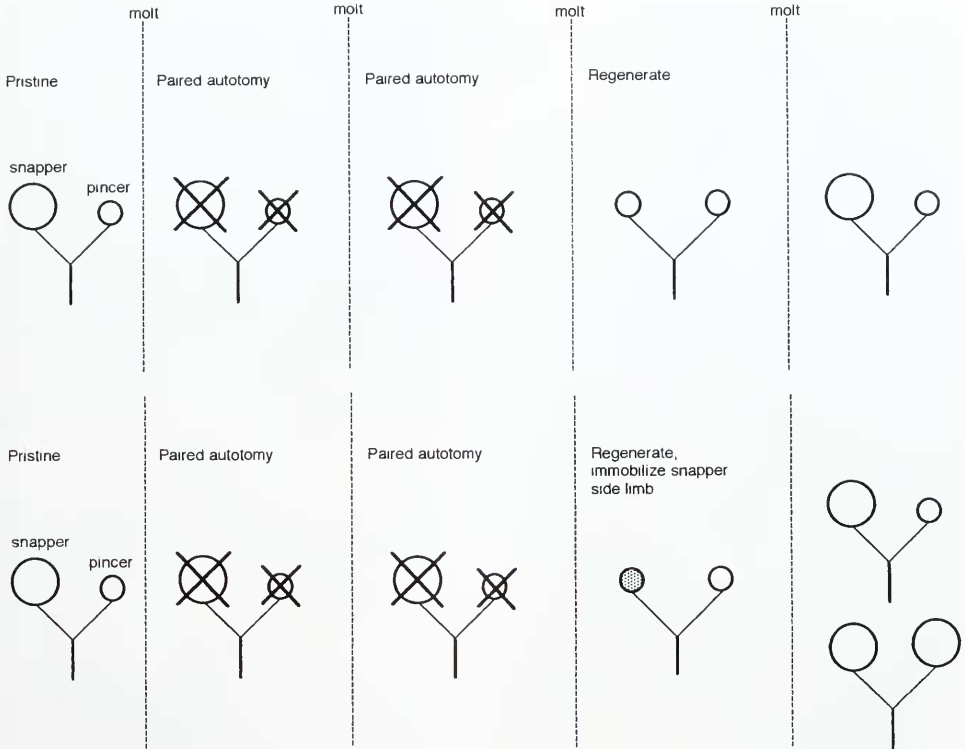
Figure 5. Pictorial representation of the paired asymmetric snapper (large circle) and pincer (small circle) claws of adult shrimp in two experiments. In the upper series the shrimps underwent two successive paired autotomies and regenerated paired pincerlike claws in the pristine configuration. The same experiment was repeated in the lower series, but after the third molt the snapper-side limb was immobilized (shaded); at the fourth molt, paired claws appeared in the pristine snapper/pincer configuration but also in a snapper/snapper configuration.

words, with some damage to the nervous system. Once the inhibition is removed the pincer continues its development to a snapper, even as late in the intermolt as the premolt stage, when the new exoskeleton is being laid down. These changes involve the exoskeleton and closer muscle composition, whereas the motor innervation (Stephens and Mellon, 1979; Quigley and Mellon, 1984; Mellon et al., 1981), sensory innervation (Govind and Pearce, 1988), and vascularization (Guchardi and Govind, 1990) occur later.

The next step in the lateralizing mechanism is for the claw advancing from the pincer to the snapper stage to exert an inhibitory influence on the regenerating contralateral claw and hold its development to the pincer stage.

Elimination of the inhibitory influence should allow the regenerating claw to develop into a snapper, and this was the case in shrimp in which removing the closer muscle in the transforming claw or transecting its nerve 2 allowed regeneration of a snapper claw on the opposite side (Young et al., 1994). We now report that simply cutting the dactyl of the transforming claw is sufficient to eliminate its inhibitory influence and permit regeneration of a snapper claw, resulting in shrimp with paired snapper claws. The first snapper arises because the pincer, released from its inhibition by snapper autotomy, continues its development to a snapper. The second snapper arises because, owing to dactylotomy of the transforming snapper, the newly regenerating claw is not restricted to a pincer stage.

Under this scheme the pincer would also advance to the snapper stage if the snapper-based inhibition was removed without loss of the snapper claw. We know that this happens readily when neural input is reduced in the snapper claw and the existing pincer continues its development to a snapper, resulting in shrimp with paired snapper claws (Mellon and Stephens, 1978; Govind *et al.,* 1988). Along similar lines is our earlier finding that cutting nerve 2 of the transforming claw (Young *et al.,* 1994) or our present finding that cutting off the dactyl of the transforming claw allows the regeneration of another snapper claw on the opposite side. But when these same surgeries were performed on a pristine snapper claw and the pincer claw was autotomized at the same time, another pincer regenerated in its place. In this case the presence of a pristine, although damaged, snapper was sufficient to inhibit regeneration to a pincer stage, but the presence of a damaged transforming snapper was not. Bearing in mind that the snapper claw has almost twice as many axons as its pincer counterpart in the pristine condition (Govind and Pearce, 1988), it is likely that dactylotomy of a transforming claw results in a much greater reduction of axons compared to the opposite side than does dactylotomy of the pristine snapper claw. Moreover, because dactylotomy affects similar structures in the transforming or pristine snapper claw, the results cast doubt on the possibility that qualitative aspects of the innervation are responsible for the different outcomes and point more to quantitative aspects. Limb regeneration in amphibians is dependent on a minimal amount of nerve in the blastema irrespective of the qualitative composition of the nerve, whether sensory or motor (Singer, 1978).

Quantitative differences in innervation between the two sides in adult snapping shrimp may also help explain the results of our experiments with paired autotomies; whether the paired autotomies were performed following reversal of asymmetry or in quick succession, the paired claws regenerated in an asymmetric configuration. The greater neural innervation to the snapper side would serve to inhibit the contralateral side even in the absence of the claws. The paired autotomy experiments suggest that claw lateralization in adult snapping shrimp has a central locus, similar to that in juvenile lobsters where differential reflex activity from the paired claws lateralizes the ganglion into major and minor sides during a critical developmental period (Govind and Pearce, 1986). Once laterality is established in juvenile lobsters it remains fixed for the entire life of the animal, and claw loss results in the regeneration of a similar claw type. Conversely, in snapping shrimp claw laterality is not fixed and can be constantly reversed. The present experiments reveal a very strong intrinsic lateralizing mechanism in the form of snapper-based inhibition that, because it operates in the absence of the claws, must reside centrally. The direction of the laterality can be readily changed by means of input from the claws in

the form of the removal of the snapper-based inhibition of the contralateral pincer claw. A useful analogy for the lateralizing mechanism is that of a seesaw in which the beam, balanced on its fulcrum, can assume one of two inclined positions but rarely a horizontal position.

Our assumption that the snapper-based inhibition of the pincer claw is neural in origin gained some support from our finding that restricting dactyl movements of the regenerating snapper claw permitted the regenerating claw on the opposite side to develop as a snapper. In these few cases, interfering with reflex activity of the regenerating snapper claw was sufficient to remove inhibition of the pincer claw. Differences in reflex activity between the two sides were also responsible for determining claw bilateral asymmetry in developing lobsters (Govind and Pearce, 1986). In snapping shrimp, differences in reflex activity are subserved by differences in numbers of axons to the paired claws (Govind and Pearce, 1988).

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